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Habitat segregation of three sympatric fossorial rodents in the Spanish Pyrenees

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Abstract

Studied the microhabitat selection among three species of sympatric fossorial voles of the subgenus *Terricola* above the timberline in the Spanish Pyrenees. The intensity of habitat use in each plot was estimated by means of the capture data and by counts of mounds made by the fossorial activity of each species. Environmental features were measured and related to the occupation level of each species by means of correlations and correspondence analysis. Results reveal some segregation between the three species in factors such as soil thickness and percentage of plant cover. *Microtus pyrenaicus,* an endemic species, prefers deep soils and dense plant cover, while *M. duodecimcostatus* seems to avoid plots with many large rocks, high slopes and prefers dense plant cover, and *M. lusitanicus* prefers low plant cover and shallow soils.

Introduction

It is generally accepted that the diversity of subterranean mammals in a given area is low, and that different species are distributed among particular habitats according to the distribution of the limiting resources (Nevo 1979). From these premises and from several considerations of the environmental features of the underground environment, Nevo (1979) predicts that no substantial overlap occurs between fossorial mammals habitats; and when two or more species coexist, the should have at least different food needs, decreasing in this way interspecific competition. Spatial coexistence among fossorial mammals would be then possible only between herbivores and insectivores (Nevo 1979).

However, instances are known of the coexistence of fossorial mammals of the same general diet, within the same order, and even the same family. For instance, fossorial mammals such as some Chrysochloridae and Bathyergidae may be found together, even in the same burrows (Hickman 1990).

Many studies have investigated the microhabitat segregation of sympatric "aboveground" small mammals (e.g. Brown and Liebermann 1973; M'Closkey and Fieldwick 1975; Dueser and Shugart 1978; Stamp and Ohmart 1978). However, to our knowledge, the only studies concerned with microhabitat segregation of subterranean mammals are those of Reichman and Jarvis (1989) and Comparatore et al. (1992). The main conclusion of the former studies is that microhabitat segregation mainly depends on the plant biomass above their burrows in the case of the three species of bathyergids (Reichman and Jarvis 1989) and on the types of soil and vegetation in the case of the two species of the genus *Ctenomys* (Comparatore et al. 1992). On the other hand, in the subterranean environment on the mountains above timberline, some other environmental resources may explain the microhabitat segregation between coexisting sympatric species of the subgenus *Terricola.*

The objective of this study was to examine the coexistence of three very similar species of fossorial rodents, *Microtus pyrenaicus, M. lusitanicus* and *M. duodecimcostatus.* All of them coexist in the supraforestal level, have similar body size, and are herbivorous species.

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Material and methods

Study area

The study plot is located in the Spanish Pyrenees, not far from the small town of Jaca, at an altitude of 2000 m above sea-level (masl), at a site where the three-mentioned species coexist. The area consists of a plot, 100 m each side on a moderate slope with a grass cover of *Trifolium alpinum, Festuca rubra* and *Nardus stricta*. The area is covered with snow between November and June of every year.

Habitat selection

The plot was subdivided into 100 squares of 10 × 10 m. Pine voles were captured alive with traps of the Sherman type and the environmental features were recorded. Data were obtained during the summers of 1990 and 1991, periods when the study area was free of snow.

The intensity of habitat use in each subplot was estimated by means of direct methods: capture data, and by indirect methods: counts of mounds made by the fossorial activity of every species. Indirect methods of investigation are needed because of the difficulty in investigating fossorial rodents in a complex habitat such as in a soil environment (Reichman and Jarvis 1989). Environmental variables recorded were: soil thickness, slope, plant cover, area covered by rocky outcrops, mean stone diameter and the percentage of wild boar rooting.

Variables were analysed by means of univariate and multivariate statistics. Correlation between habitat variables and the number of mounds at each sample plot were tested by Spearman's rank correlation coefficients (Siegel 1986) because distributions of values were not normal. We have applied a correspondence analysis for the segregation of the different species. Habitat variables were subdivided into a number of categories. Subdivision of a parameter was determined by arbitrary evaluation of the width of the ecological gradient existing in the study area. A contingency table was created by expressing habitat variables as frequencies of occurrence of *Microtus* species. Calculation was based on the program SYN-TAX III/PC (Podani 1988).

Results

Spearman correlations

Total number of captured voles was 107 (65 *Microtus pyrenaicus*, 27 *M. duodecimcostatus* and 15 *M. lusitanicus*); 1153 soild mounds were found within the plot; from these, 393 were made by *M. pyrenaicus*, 640 by *M. lusitanicus* and 120 by *M. duodecimcostatus*.

Before any other analysis, we compared the capture level and the number of earth mounds on each subplot, as a way of calibrating the two estimates of habitat use. Both

Spearman rank correlation coefficients between habitat variables and number of mounds at each plot

(n = 1153)

Species	*M. pyrenaicus*		*M. lusitanicus*		*M. duodecimcostatus*	
	r_s	p	r_s	p	r_s	p
Number of mounds of *M. p.*	1.0000	1.0000	−0.2694	0.0073**	0.0420	0.6760
Number of mounds of *M. l.*	−0.2694	0.0073**	1.0000	1.0000	−0.0733	0.4665
Number of mounds of *M. d.*	0.0420	0.6760	−0.0733	0.4655	1.0000	1.0000
Average soil depth	0.3527	0.0004***	−0.0695	0.4894	0.0992	0.3236
Maximum soil depth	0.2267	0.0241*	−0.0136	0.8920	0.0841	0.4028
Minimum soil depth	0.3040	0.0025**	−0.0737	0.4631	0.1507	0.1337
% cover of exposed rock	−0.1685	0.0936	0.0514	0.6088	−0.2508	0.0126*
Average slope	−0.1466	0.1447	−0.0948	0.3457	−0.1849	0.0658
% cover of vegetation	0.3658	0.0003***	−0.3679	0.0003***	0.0921	0.3595
% cover of wild boar rooting	−0.0981	0.3293	0.5309	0.0000****	−0.0615	0.5407
Average diameter of rocks	0.1452	0.1485	−0.0627	0.5325	−0.2526	0.0120*

**** $p < 0.0001$; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

variables were highly correlated ($r_s = 0.48$; $p < 0.0001$; $n = 100$). The low value of the Spearman coefficient may be due to the different time scale of both variables: while capture numbers reveal pine vole activity over a short span of time, the number of soil mounds is a cumulative variable related to the average habitat use during a long period. The second variable is preferred for habitat studies. The results of the correlation between variables are summarized in the table.

Microtus pyrenaicus

Habitat use of this species is positively correlated to plant cover ($r_s = 0.37$; $p < 0.0001$) and to soil depth ($r_s = 0.35$; $p < 0.0001$). Negative but not significant correlation exists between slope ($r_s = -0.15$; $p = 0.14$) and percentage of rocks in the subplot ($r_s = -0.17$; $p = 0.09$). It appears as if this species selected the best places to burrow, where soil is deeper and flatter, but, although several variables seems linked to this species, not one of them shows a correlation strong enough to allow prediction of the presence of the species as a function of only this variable. Therefore, the distribution of *Microtus pyrenaicus* should depend on an interaction between the four above-mentioned variables. Influence of different variables can be clearly seen in the figure. While the species seems to prefer lower slopes, it is found also in steep places, with slopes surpassing 40 %.

Microtus lusitanicus

The only positive correlation shown by this species is to the percentage of wild boar rooting ($r_s = 0.53$; $p < 0.0001$). A negative correlations exists between abundance of the species and plant cover ($r_s = -0.37$; $p < 0.01$).

Moreover, *M. lusitanicus* is negatively correlated to the abundance of *M. pyrenaicus* ($r_s = 0.27$; $p < 0.01$). It appears as if *M. lusitanicus* chose, or was forced to select, marginal habitats, not preferred by the former species. Association between this species and patches of wild boar activity is striking. Even where these patches do not coincide with active vole colonies there are signs of an old deserted colony of *M. lusitanicus*. Wild boar could be a predator of voles, and seems to prefer this species, due perhaps to accesibility offered by the more superficial burrows that *M. lusitanicus* makes.

M. lusitanicus inhabits sites with shallow soils, low proportion of rocky outcrops, high slopes and medium to sparse plant cover (Fig.).

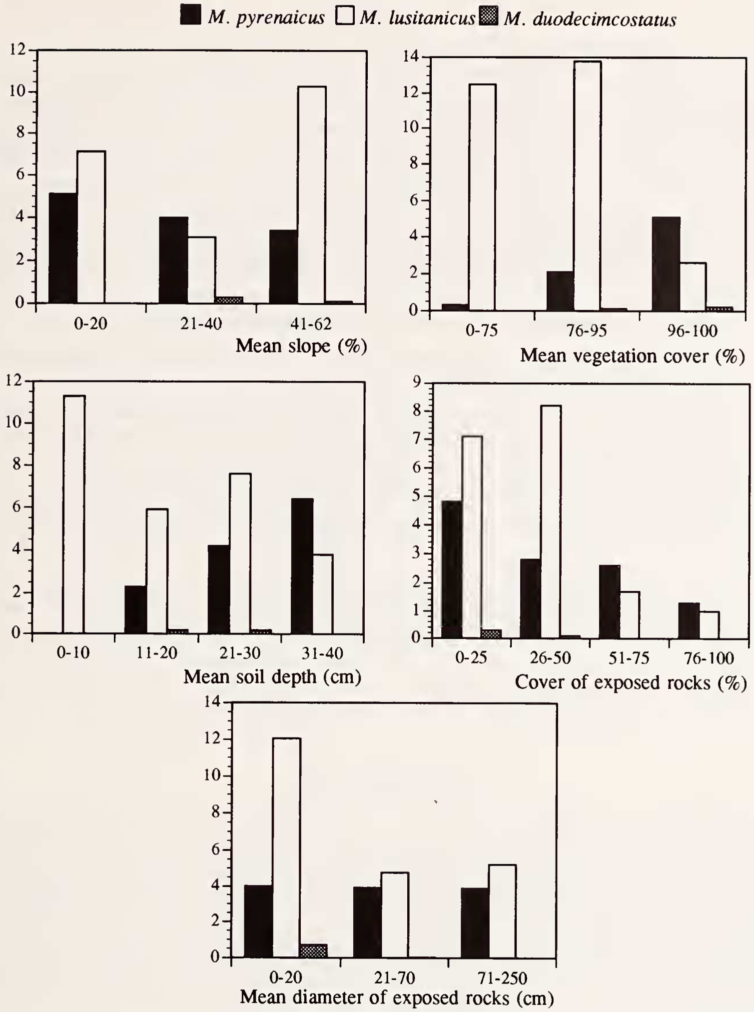
Microtus duodecimcostatus

This is a lowland species which in the study area almost reaches its altitudinal limit. It occurs in low abundance, and the number of both captures and mounds is small. The only significant correlations are negative, and rather low: there is a negative relationship between the abundance of the species and both the surface covered by rocks ($r_s = -0.25$; $p = 0.012$) and the average diameter of rock outcrops ($r_s = -0.25$; $p < 0.05$). As seen in the figure, the species seems to select soils of intermediate thickness, low presence of rocks, moderate slope and dense plant cover.

Correspondence analysis

The first axis explains approximately 81 % of the variance, and the first two axes accounted for the total inertia (100 %). The first axis seems to be linked to plant cover and soil thickness; the second axis is not so clear as the former one, and seems to be linked to the percent of rock outcrops and to gravel diameter. Wild boar rooting activity seems also linked to the first axis.

The first axis segregates the three species along the variables related with the slope, plant



Mean number of mounds in each plot, in Los Lecherines (2000 masl) related to the environmental features recorded

cover and soil depth, pointing to *M. pyrenaicus* as the species that can live in intermediate conditions, *M. duodecimcostatus* being associated with the deeper soils, and the highest values of plant cover; and *M. lusitanicus* associated with the opposite values of this axis. The second axis segregates *M. pyrenaicus* from the other species, *M. pyrenaicus* being the species that can live in plots with abundant and sizeable rocks, while the other species are associated with the opposite values of this axis.

Discussion

Microtus pyrenaicus appears to be rather flexible in its habitat use, being found at sites with very different features. *M. lusitanicus* is relegated to the thinnest soils and to sites with sparse plant cover, while *M. duodecimcostatus* is found only in the opposite microhabitats, associated with high scores of plant cover and soil thickness, and with low slopes. The first species is also the only one that tolerates the use of rocky terrain.

Habitat segregation in sympatric fossorial mammals does not always rely on the partitioning of food resources, as implied by Nevo (1979). The unexpected spatial overlapping among three species of taxonomically related fossorial voles in the supraforestal level of the Spanish Pyrenees, and the three sympatric species of molerats in the Cape Province of South Africa (Reichman and Jarvis 1989) are a clear contra-example.

Our results suggest that *Microtus pyrenaicus* selects advantageous sites for burrowing, where soil is deep and flat. *M. duodecimcostatus* occurs at sites where competition with other species is low, or where environmental features are still adequate (thick and flat soil also), and *M. lusitanicus* at sites where the plant cover is sparser and where there are fewer interactions with *M. pyrenaicus*. *M. lusitanicus* is strongly associated with the activity of the wild boar, probably because it is most preyed on by the wild boar, in turn, perhaps due to its burrowing in the shallowest soils.

The highly complex topographic relief of the mountain environment produces an increase in diversity of mammalian species, as has already been observed for mammals in the United States (Simpson 1964), and particularly the epigeal *Microtus* species in North America (Rose and Birney 1985). The coexistence of three sympatric fossorial rodents in the Spanish Pyrenees could, therefore, be the final product of a very complex subterranean environment in the mountains, where soil depth, plant cover and slopes are very heterogeneous. The underground environment is very different to that of *Spalax ehrenbergi* studied by Nevo (1979) in arid environments, where the underground habitat is structurally simple, and where the competition for food resources may lead to competitive exclusion. Thus, an increase in complexity of the underground environment at high altitudes allows the sympatry of the pine voles, while the most important variables segregating the microhabitat of these species are soil depth and plant cover.

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Zusammenfassung

Habitatwahl bei drei Arten von Kurzohrmäusen in den spanischen Pyrenäen

Drei Arten von Kurzohrmäusen, die in den spanischen Pyrenäen oberhalb der Baumgrenze syntop vorkommen, wurden auf Unterschiede in der Wahl des Lebensraumes hin untersucht. Die Dichte jeder Art in den Probeflächen wurde anhand der Mittelwerte von Fängen und der Anzahl aufgeworfener Hügel abgeschätzt. In den gleichen Probefeldern wurden verschiedene Umweltmerkmale registriert und mit den Vorkommenshäufigkeiten der drei Arten verglichen. Die Ergebnisse zeigen deutliche Unterschiede, vor allem in den Variablen Bodentiefe und Pflanzenbedeckung. *Microtus pyrenaicus*, eine endemische Art der Pyrenäen, bevorzugt tiefen, erdreichen Boden mit hoher Vegetationsdichte. *M. duodecimcostatus* scheint in Gebiete mit groben Felsen, stark abschüssigen Hängen und Gegenden mit hoher Vegetationsdichte auszuweichen, während *M. lusitanicus* anscheinend Flächen mit geringer Vegetationsdichte und flachgründigen Böden aufsucht.

References

Brown, J. H.; Lieberman, G. A. (1973): Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology **54**, 788–797.

Comparatore, V. M.; Agnusdei, M.; Busch, C. (1992): Habitat relations in sympatric populations of *Ctenomys australis* and *Ctenomys talarum* (Rodentia, Octodontidae) in a natural grassland. Z. Säugetierkunde **57**, 47–55.

Dueser, R. D.; Shugart, H. H. Jr. (1978): Microhabitats in a forest-floor small mammal fauna. Ecology **59**, 89–98.

Hickman, G. C. (1990): The Chrysochloridae: studies toward a broader perspective of adaptation in subterranean mammals. In: Evolution of Subterranean Mammals at the Organismal and Molecular Levels. Ed. by E. Nevo and O. Reig. New York: Alan R. Liss. Pp. 23–48.

M'Closkey, R. T.; Fieldwick, B. (1975): Ecological separation of sympatric rodents (*Peromyscus* and *Microtus*). J. Mammalogy **56**, 119–129.

Nevo, E. (1979): Adaptative Convergence and Divergence of Subterranean Mammals. Ann. Rev. Ecol. Syst. **10**, 269–308.

Podani, J. (1988): SYN-TAX III, User's Manual, Abstracta Botanica **12** (Sup. 1), 1–182.

Reichman, O. J.; Jarvis, J. U. M. (1989): The influence of three sympatric species of fossorial mole-rats (Bathyergidae) on vegetation. J. Mammalogy **70**, 763–771.

Rose, R. K.; Birney, E. C. (1985): Community Ecology. In: Biology of New World *Microtus*. Ed. by R. H. X. Tammarin. Spec. Publ. No. 8, The American Society of Mammalogists. Pp. 310–339.

Siegel, S. (1986): Estadística no parámetrica. México D. F.: Editorial Trillas.

Simpson, G. G. (1964): Species density of North American Recent Mammals. Syst. Zool. **13**, 57–73.

Stamp, N. E.; Ohmart, R. D. (1978): Resource utilization by desert rodents in the lower Sonoran desert. Ecology **59**, 700–707.

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